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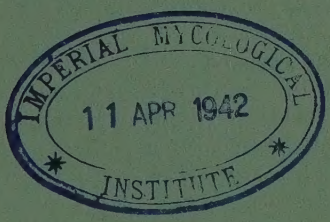

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THE BOTANICAL REVIEW

VOL. I APRIL, 1935 No. 4

PHYSIOLOGIC SPECIALIZATION OF THE PARASITIC FUNGI[1]

GEORGE M. REED

Curator, Brooklyn Botanic Garden

The discovery by Eriksson (15) of the existence of specialized races of rusts is one of the most important developments in plant pathology. His demonstration that the morphological species of *Puccinia graminis* Pers., *P. glumarum* (Schmidt) Erikss. & Henn., *P. dispersa* Erikss. & Henn. and *P. coronata* Cda. consist of subdivisions which can be distinguished from one another by their ability to grow on some hosts and not on others, has stimulated many workers to investigate the extent and significance of host specialization among the various groups of parasitic fungi. In 1918, I (59) published a fairly complete review of the field, listing 174 papers which described results with the rusts, powdery mildews, downy mildews and other fungi. Since then, through studies of many investigators, the literature on this subject has greatly increased.

The primary basis for evidence of physiologic specialization is the behavior of different collections of parasitic fungi on particular hosts. Recognized hosts of a morphological species of fungus may be infected by some collections and not by others. If conidia of *Erysiphe graminis* DC. from wheat are sown on wheat, barley, oats and rye, the wheat is infected but not the other three cereals. If conidia from barley are sown on the four cereals, only the barley becomes infected. Thus, the mildews on wheat and barley are clearly differentiated from each other by their ability to establish themselves on definite hosts.

Obligate parasitic fungi, such as the rusts and powdery mildews, must be cultured on living plants, and one of the problems is the selection of suitable hosts for differentiation of specialized races,

[1] Brooklyn Botanic Garden Contributions No. 71.

if such exist. Races may also be distinguished by the type and degree of infection. Stakman and Levine (79) have developed a method for detecting physiologic forms of *Puccinia graminis,* which has come into general use. Six types of infection are recognized: 0—immune; 1—very resistant; 2—moderately resistant; 3—moderately susceptible; 4—very susceptible; X—heterogeneous. Different degrees of infection of most of these types serve further to distinguish the reaction of the forms. Differences have also been noted in rate of development of the telial stage of rusts on definite hosts by various collections. Sometimes growth on seedlings and adult plants may also serve to distinguish races.

Many parasitic fungi, such as smuts and various species and genera of the Ascomycetes and Imperfect Fungi, however, may be cultured on laboratory media, and it is possible to distinguish strains or races by differences in their growth characteristics. Such strains are distinguished as "cultural races" from the "pathogenic races," which are differentiated by their capacity for infecting living plants. In culture, it is possible to observe the influence of various substances, such as sugars and other chemicals, on rate and extent of growth. Character of growth, its consistency, whether uniform or sectoring, topography of the surface, color, etc., are all characters which may be used for distinguishing between different strains.

The most extensive studies on physiologic specialization have been made on various parasites of the cereals—rusts, smuts and powdery mildews. The reasons are rather obvious. For one thing, each of the main groups of cereals consists of a large number of varieties which have been derived from many sources and these differ widely in their various agronomic and physiologic characters. Further, the cereals are easily grown and subjected to varied experimental conditions. Finally, the economic importance of cereal crops is undoubtedly a major factor. The seriousness of the various rusts, smuts and other diseases of these crops has led to extensive investigation in all phases of their pathology.

PHYSIOLOGIC SPECIALIZATION IN THE CEREAL RUSTS

Eriksson (15) separated *Puccinia graminis* into six "formae speciales": *avenae, secalis, tritici, airae, agrostidis* and *poae.* He further recognized *P. phlei-pratensis* as a distinct species. *P. glumarum*

was found to consist of five specialized forms: *tritici, secalis, elymi, agropyri* and *hordei. P. dispersa* consisted of four specialized forms: *secalis, agropyri, bromi* and *tritici.* Finally, *P. coronata* was separated into six specialized forms: *avenae, alopecuri, festucae, lolii, calamagrostis* and *melicae.* Investigations of recent years, however, have resulted in the subdivision of many of these "formae speciales" into secondary groups. In 1917, Stakman and Piemeisel (83) discovered that *Puccinia graminis tritici* Erikss. and Henn. consisted of at least more than one specialized race or "physiologic form." Stakman and Levine (79), in 1922, announced 37 physiologic forms, and in 1934, Stakman, Levine, Cotter and Hines (82) mentioned 127. To this number, Tu (88) has added 6 additional ones for China. According to Mains (40), *Puccinia rubigo-vera* (DC.) Wint. consists of 56 races, based in part upon the relation between telial and aecial hosts. One of these races, *P. rubigo-vera tritici* (Erikss. and Henn.) Carleton, is further separated into 53 sub-groups or physiologic forms.

Some of the most significant advances on physiologic specialization of cereal rusts are given in the accompanying table.

GEOGRAPHICAL DISTRIBUTION OF RUST RACES

Standardized methods in the study of biologic forms of rusts have been developed. Stakman and Levine (79) introduced the use of twelve varieties of wheat for differentiating the forms of *Puccinia graminis tritici.* Mains and Jackson (43) employed eleven varieties of wheat in the study of biologic forms of *P. rubigo-vera tritici.* Special varieties and strains of rye, oats and barley have also been employed. Use of the same set of differential hosts in different countries has made it possible to compare the results of studies on physiologic specialization.

Distribution of physiologic forms of *Puccinia graminis tritici* has been studied by a number of workers. Recently, Stakman, Levine, Cotter and Hines (82) recorded 82 physiologic forms, identified from more than 8,000 cultures. Form 36 occurred most commonly and was most widely distributed and was found in 11 States. Form 38 was isolated from collections made in 7 States. Some forms were collected only once. Newton and Johnson (49) stated 41 physiologic forms have been isolated in Canada between 1919 and 1930. Different physiologic forms predominated in dif-

PHYSIOLOGIC FORMS IN THE CEREAL RUSTS

Fungus	*No. of Races*	*Year*	*Authority*	*Country*
Puccinia anomala	2	1930	Mains (38)	U. S.
	4	1931	Brown (7)	Canada
	8	1931	Hey (29)	Germany
Puccinia coronata avenae	2	1919	Hoerner (30)	U. S.
	4	1927	Parson (54)	U. S., Canada
	4	1930	Peturson (55)	Canada
	33	1930	Frenzel (19)	Germany
	33	1933	Murphy (47)	U. S.
Puccinia glumarum ..	4	1930	Allison and Isenbeck (2)	Europe
	5	1931	Wilhelm (94)	Europe
Puccinia graminis avenae	4	1923	Stakman *et al.* (80)	U. S.
	5	1925	Bailey (4)	U. S., Sweden
	5	1929	Waterhouse (91)	Australia
	5	1930	Tedin (84)	Sweden
	2	1931	Verwoerd (89)	South Africa
	9	1933	Gordon (24)	Canada
Puccinia graminis secalis	2	1923	Levine and Stakman (37)	U. S.
	14	1932	Cotter and Levine (13)	U. S.
	2	1931	Verwoerd (89)	South Africa
Puccinia graminis tritici	1	1917	Stakman and Piemeisel (83)	U. S.
	37	1922	Stakman and Levine (79)	U. S.
	8	1929	Waterhouse (91)	Australia
	2	1931	McDonald (44)	Central Africa
	8	1931	Verwoerd (89)	South Africa
	41	1932	Newton and Johnson (49)	Canada
	6	1934	Tu (88)	China
	127	1934	Stakman *et al.* (82)	World
Puccinia rubigo-vera tritici	12	1926	Mains and Jackson (43)	U. S.
	4	1928	Scheibe (75)	Central Europe
	2	1929	Waterhouse (92)	Australia
	8	1930	Scheibe (76)	Central Europe
	3	1930	Wellensiek (93)	Netherlands
	7	1931	Dodoff (14)	Bulgaria
	6	1931	Tscholakow (87)	Europe
	1	1930	Johnston (34)	U. S.
	26	1932	Johnston and Mains (35)	U. S.
	10	1932	Radulescu (58)	Rumania
	53	1933	Mains (40)	World
Puccinia sorghi	7	1928	Stakman *et al.* (78)	U. S.

ferent years; some forms were commonly isolated while others were rare.

Waterhouse (91) records the isolation of 8 biologic forms in Australia, 7 of which were restricted to that country while one was identical with a physiologic form found in the United States. Tu (88) isolated 6 forms in China, 2 of which are identical with American forms, and 4 are new. McDonald (44) and Verwoerd (89), in Africa, have identified their physiologic forms with similar ones in the United States.

Mains and Jackson (43), in 1926, described 12 biologic forms of *Puccinia rubigo-vera tritici*. Scheibe (75, 76), in 1928 and 1930, isolated 12 forms, 11 of which differed from those of Mains and Jackson. Dodoff (14), in 1931, isolated 7 forms in Bulgaria, only one of which was new.

Frenzel (19), in Europe, isolated 33 biologic forms of *Puccinia coronata avenae* out of only 27 collections. Murphy (47), during the period 1927 to 1932, isolated 33 physiologic forms of crown rust of oats from 533 collections obtained in 29 States in the United States, 3 States of Mexico and 3 Provinces of Canada.

Rudorf and Job (71) have found that the physiologic forms of *Puccinia graminis tritici* in the Argentine are different from those in North America. On the other hand, of the 5 forms of *P. rubigo-vera* isolated, 2 seemed to be identical with the North American forms 5 and 9.

PHYSIOLOGIC SPECIALIZATION IN THE SMUTS

It is interesting to note that in my review of physiologic specialization, published in 1918 (59), no experimental evidence of this phenomenon in the smuts was recorded. In fact, it was not until 1921 that Zillig (95) definitely established the existence of specialized races in *Ustilago violacea* (Pers.) Fuck. by inoculation experiments. The first experimental evidence of specialization in cereal smuts was published in 1924 when Faris (17) described five races of *U. hordei* (Pers.) K. & S., separated by their reaction on certain varieties of barley, and Reed (60) published data that showed that both the loose and covered smuts of oats were differtiated into distinct races. The latter used spores from each species of smut of oats, collected in Missouri and in Wales, for inoculating a series of oat species and varieties. Distinct differences

in infection capacity of the collections from the two countries were observed. His results were confirmed in the following year by Miss Sampson (72). In 1927, Reed (61) described two new races of loose smut of oats occurring on red oat varieties, which hitherto had shown a high degree of resistance to the smuts; one of the new races attacked Fulghum, as well as a number of oat varieties be-

Fungus	*No. of Races*		*Year*	*Authority*
Sphacelotheca sorghi (Link) Clint. ..	2		1927	Tisdale *et al.* (85)
	5		1932	Melchers *et al.* (46)
Sorosporium reilianum (Kuehn) McAlp.	2		1927	Reed *et al.* (66)
Tilletia laevis Kuehn, and *T. tritici* (Bjerk.) Wint.	*Laevis* 4	*Trit.* 6	1928	Reed (63)
	3	2	1927	Rodenhiser and Stakman (69)
	2	3	1928	Gaines (20)
		1	1930	Reichert (67, 68)
	2	3	1931	Holton (31)
	6	4	1931	Bressman (6)
	5	1	1931	Aamodt (1)
	2	5	1933	Gaines and Smith (21)
	6	7	1933	Flor (18)
	7		1934	Melchers (45)
	Ave.	*Lev.*		
Ustilago avenae (Pers.) Jens., and *U. levis* (K. & S.) Magn.	2	2	1924	Reed (60)
	2	2	1925	Sampson (72)
	2		1927	Reed (61)
	11	5	1929	Reed (64)
	2	1	1932	Reed and Stanton (65)
	1	1	1929	Sampson (73)
Ustilago hordei (Pers.) K. & S. ...	5		1924	Faris (17)
Ustilago tritici (Pers.) Jens.	4		1930	Grevel (26)
Ustilago zeae (Beck.) Ung.	7		1926	Christensen and Stakman (11)

longing to the group of common oats. The second race was rather sharply confined to Red Rustproof and its close relatives, although it was able to pass on to the common oat variety, Canadian. Reed (64), Reed and Stanton (65), Sampson (73), and Nicolaisen (52, 53) have added further evidence of specialization in the oat smuts.

In 1924, Faris (16) suggested, on the basis of some of his experiments, that physiologic specialization occurred in *Tilletia laevis*

Kuehn and *T. tritici* (Bjerk.) Wint. Reed (62), in 1927, demonstrated conclusively that Martin wheat was susceptible to certain collections of bunt and resistant to others; in 1928 (63) his detailed results were published in which 6 races of *T. tritici* and 4 races of *T. laevis* were definitely established. Rodenhiser and Stakman (69), in 1927, published some data indicating the existence of 3 races of *T. laevis* and 2 of *T. tritici,* and in 1928, Gaines (20) and Roemer (70) reported that a collection of *T. tritici* from Washington State differed from another collection from Germany in its capacity for infecting certain varieties of wheat.

Demonstration of specialization in cereal smuts has stimulated many investigators in various places. Some of the results already obtained are presented in tabular form on preceding page.

PHYSIOLOGIC SPECIALIZATION IN THE POWDERY MILDEWS AND OTHER FUNGI

There is very extensive literature on specialization in powdery mildews, downy mildews, various Ascomycetes and Fungi Imperfecti which it is impossible even to mention here. A very brief reference to a few papers will indicate some of the progress that has been made:

Fungus	*No. of Races*	*Year*	*Authority*
Albugo candida (Pers.) Rouss ..	5	1934	Togashi and Shibasaki (86)
Albugo ipomoeae-panduranae (Schw.) Sw.	2	1928	Ciferri (12)
Albugo tragopogonis (DC.) S. F. Gray	6	1927	Pfister (57)
Colletotrichum lindemuthianum (Sacc. & Magn.) Bri. & Cav. ..	5	1928	Budde (8)
	12	1931	Peuser (56)
	34	1932	Schreiber (77)
Erysiphe communis Grev.	26	1925	Hammarlund (27)
Erysiphe graminis DC. f. sp. *hordei*	5	1930	Mains and Dietz (42)
tritici	2	1933	Mains (39)
Erysiphe horridula Rab.	7	1922	Blumer (5)
Helminthosporium gramineum Rab.	20	1934	Christensen and Graham (10)
Phyllactinia guttata Lév.	6	1925	Hammarlund (27)

One of the particularly significant features in connection with specialization of powdery mildews is the discovery by Mains (39), and Mains and Dietz (42), that *Erysiphe graminis tritici* and *E. graminis hordei* may be further subdivided into physiologic forms, thus paralleling the results obtained with many cereal rusts.

MORPHOLOGICAL VARIATIONS IN SPECIALIZED RACES

Extensive investigations have been made on the question as to whether these specialized races may be distinguished by differences in spore size or other morphological characters. Levine (36) published detailed results with the physiologic forms of *Puccinia graminis tritici* and has found minor variations in spore size and shape which seem to be distinctive of definite races. Blumer (5) has distinguished some of the specialized forms of *Erysiphe horridula* by their spore measurements. Togashi and Shibasaki (86) have separated *Albugo candida* into the varieties *macrospora* and *microspora*, based upon differences in spore size, and they have further found that the first variety consisted of two distinct biologic forms, and the second variety, of three. Savulescu and Rayss (74) recorded 8 forms of *A. candida* on the basis of minute differences in conidial measurements. One of the most extensive studies of this character was made by Gäumann (22) on the genus *Peronospora*. He has split up several of the species on the basis of minor variations in spore size and shape. *Peronospora parasitica* (Pers.) Fries, for example, has been separated into 25 groups which he has raised to specific rank.

It is a question to what extent these minor variations in spore size and shape are significant. Many of the differences recorded are exceedingly minute and it may be doubted whether they have value at all comparable to that obtained through inoculation experiments.

The fact that there are these minor differences, however, naturally raises the question as to the distinction between a physiologic race and a morphological species or variety. Apparently, there is no real sharp line of separation. Many species of parasitic fungi can readily be recognized by morphological characters; in other cases, differences are relatively indefinite. Many of the "formae speciales" of *Puccinia rubigo-vera* have been recognized in books as so-called species. Arthur, in his "Manual of the Rusts in United

States and Canada," has called attention to the fact that, in the determination of a rust, one of the most important factors is the correct name of the host. It is very doubtful whether many of the entities listed as species could be accurately identified without knowledge of the plant upon which the material was collected.

INFLUENCE OF ENVIRONAL FACTORS ON THE REACTION OF DIFFERENTIAL HOSTS TO VARIOUS PHYSIOLOGIC FORMS OF RUSTS

Waterhouse (91), in 1929, made the significant discovery that the specific reaction of a host to certain physiologic forms of *Puccinia graminis tritici* varied under winter and summer conditions. In some cases, he found that a given variety was quite susceptible in hot summer months and resistant in winter months to certain specialized forms. Marquis varied from complete susceptibility to forms 46 and 55 during summer to moderate resistance in winter. This variety is a differential host for forms 45 and 55; its usual reaction to 45 is moderate resistance and, to 55, high susceptibility. If, however, the environal conditions change its reaction with form 55 from susceptibility to moderate resistance, the line of separation between the two forms largely disappears.

Waterhouse (91) found similar variations in the behavior of certain forms of *Puccinia graminis avenae, P. triticina* and *P. simplex*. With the latter species, 14 susceptible varieties of barley gave the same results during both summer and winter. However, 8 varieties resistant under winter conditions were susceptible during the summer period.

Gordon (23, 24), in 1930 and 1933, published similar data on certain forms of *Puccinia graminis avenae*. White Russian, Richland, Victory and Joanette showed no significant differences in their reaction to physiologic forms 2, 6, 7 and 8 when grown at four different temperatures from 57.4° F. to 75.4°. The Joanette strain, however, was very resistant to forms 1, 3, 4 and 5 at low temperatures and susceptible at high. Peturson (55), in 1930, found that Red Rustproof oats was resistant to form 4 of *Puccinia coronata avenae* at 57° F. and susceptible at both 70° and 77°. Four other varieties, Green Mountain, White Tartar, Green Russian and Sterilis Selection were fully susceptible at all three temperatures while Ruakura was resistant. Johnson (32) obtained similar results with forms of *P. graminis tritici*. Other en-

vironal factors have also been studied and found to have a definite effect.

Goulden, Newton and Brown (25), in 1930, stated that certain wheat varieties showed no essential differences in reaction to 16 physiologic forms of *Puccinia graminis tritici* in the seedling and mature plant stage. A few varieties, however, varied markedly in resistance in the two stages of plant growth.

These results are extremely significant in the problem of differentiating specialized races and they emphasize the fundamental importance of environal factors in the interplay of host and parasite.

In cereal smuts, environal conditions are known to have a determining influence upon infection and it is necessary to supply favorable conditions for infection in order to determine the real reaction of a variety. Much of the work on cereal smuts has been done by sowing seed in the open and depending upon chance combination of favorable environal conditions. Usually, low percentages of infection have resulted and it is doubtful whether much significance can be attached to results based upon slight variations in percentage of infection of varieties under such conditions.

The recognition of the part played by environal factors is of significance in connection with the study of inheritance of disease resistance. Waterhouse (91), in 1929, reported that certain barley crosses gave different results in winter and summer months. Some families which in winter had given him a normal ratio of three resistant to one susceptible, in summer months failed to show the expected segregation. Harrington (28) found that a series of progenies of a cross of Marquillo x Marquis showed susceptibility as dominant with form 21 of *Puccinia graminis tritici* at a high temperature, while at a low temperature resistance was dominant. Mains (41) has also recorded that hybrids between Michigan Amber and Chinese wheats were difficult to classify in their reaction to a race of *Erysiphe graminis tritici* when grown in the spring. In winter time, however, it was comparatively easy to classify the hybrid lines. The Michigan Amber parent was resistant in winter while more or less susceptible in spring.

THE CONSTANCY OF SPECIALIZED RACES

It is an important question whether the races, forms, biotypes, etc., which are isolated through reaction of differential hosts, are

true-breeding constant entities. Isolations cultured on living hosts have shown remarkable uniformity over a period of successive generations, frequently covering years of time. The same sets of varieties have been utilized in different parts of the world for differentiating cereal rust physiologic forms and, so far as the particular varieties used are concerned, the forms may be identified in widely separated countries.

It is also interesting to note the ease with which two or more races may be separated from mixed collections of parasitic fungi. Frenzel (19) isolated 33 distinct races of crown rust of oats from 27 different collections. In rust surveys carried out in the United States and Canada, some of the same forms have been isolated year after year, frequently from widely separated localities. The Missouri races of loose and covered smuts have been grown annually for more than twenty years and, throughout that period of time, have shown a constant behavior on given varieties of oats. They have been artificially mixed and used for inoculating oat varieties, and the two species, with their usual capacities for infection, have again been secured. Mixtures of different races of smuts have been collected in the field. One of the best illustrations is the fact that a collection of loose smut was received from Texas and used to inoculate certain oat varieties. As a result of the experiments, the original mixture was found to consist of two distinct new races of loose smut, one capable of infecting Fulghum and the other, Red Rustproof.

In the study of racial specialization, the question of bridging hosts has occupied a prominent place. Such a host was defined as a plant which enabled a specialized race to extend its normal range. A fungus growing on one plant might be able to infect a second slightly and a third not at all. By growing the parasite on the second variety, it was supposed to acquire an ability to pass successfully over to the third. At the present time, however, there seems to be no clear-cut evidence that such a type of adaptation really occurs. There has been no demonstration of extension of range of hosts through acquired pathogenicity. In smuts, a low percentage of infection of a particular variety is sometimes obtained. Spores collected on such a variety and resown sometimes give a very high percentage of infection. Apparently, what has really been done is to separate out two specialized races from the original mixture.

In contrast to the apparent constancy of races on living plants, passing reference may be made to the behavior of races that are isolated on artificial media. Many investigators have published data on cultural behavior of various species of smuts, and marked variation in cultural behavior of the isolations with reference to color, consistency, topography of the surface, rate of growth, sectoring, etc., have been recorded. The significance of these variations is by no means clear. It has been assumed by some to be associated with hybridization and possibly mutation, resulting in the formation of new specialized strains.

Specialized races of cereal rusts are based primarily on cultures of urediospores. These rusts are heteroecious and their complete cycle includes stages on both cereals and barberry or other aecial host. In the life cycle, urediospores are binucleate and give rise to binucleate mycelium. In other words, rust races are characteristically based upon the diploid stages of the parasite.

On the other hand, powdery mildew races are based upon inoculation experiments with conidia and, so far as their position in the life history of the fungus is concerned, conidia are haploid in nature and serve to perpetuate by successive generations the haploid phase of the powdery mildew. Ascospores of mildews have also been used for inoculations. These, however, are also haploid in nature.

In smuts there is a different situation. Young chlamydospores are binucleate and, in some stage of their development, nuclear fusion occurs. When the chlamydospores germinate, a promycelium is formed which gives rise to uninucleate sporidia. However, before infection of the host takes place, fusion of two conidia is necessary although, in the corn smut, so-called solopathogenic lines have been demonstrated by Christensen (9). The inoculum ordinarily used in smuts is the diploid chlamydospore but, during the few hours between inoculation and infection, the parasite passes through the haploid stage back again into the diploid.

ORIGIN OF NEW SPECIALIZED RACES

The origin of new specialized forms has always attracted attention. It is evident that specialization is practically a universal phenomenon in parasitic fungi and the number of races that may be isolated appears to be unlimited. So far as cereal rusts are con-

cerned, evidence is accumulating that specialized forms originate on the barberry through hybridization. Newton, Johnson and Brown (50, 51) selfed 8 physiologic forms of *Puccinia graminis tritici* by mixing the pycnial nectar on barberry leaves. Isolations were then made from the aecia and the reaction of the cultures on wheat varieties determined. They found that physiologic form 9, when selfed, gave rise only to form 9; thus it was homozygous. On the other hand, 7 other forms each gave rise to 2 or more biologic forms; in fact, from the selfing of form 53 they obtained 18 different known biologic forms of the rust. These workers have also recorded some data on crossing different forms. A cross between physiologic form 9a and 36 gave, in the F_1 generation, form 17a; in the F_2 generation, physiologic forms 1, 1a. 11, 11a, 15, 17, 17a, 36, 36a, 57a and 85 were secured. Further data are given by Johnson, Newton, and Brown (33).

Stakman, Levine and Cotter (81) made 5 crosses between form 36 of *Puccinia graminis tritici* and *P. graminis agrostidis*. Two of the crosses gave negative results. From one cross, 4 physiologic forms of *tritici* were isolated; from a second, 1 form; and from a third, 9 forms. Three of the forms isolated were hitherto unknown. It is interesting that no physiologic forms of *P. graminis agrostidis* were recovered. Crosses between physiologic forms of *P. graminis tritici* and *secalis* were also studied.

Very few mutations in rust physiologic forms have been recorded. Newton and Johnson (48) reported a color mutation in physiologic form 9 of *Puccinia graminis tritici*; a race with orange color urediospores appeared after six uredinial generations. The new form was identical in its pathogenicity and both forms have since been cultured several years without showing any further changes.

Waterhouse (90), in 1929, also obtained a color variant in one of his cultures of form 34 of *Puccinia graminis tritici*. Stakman, Levine and Cotter (81) observed the appearance of a new form in cultures of form 1 of *P. graminis tritici* after more than thirteen years. It was identified as physiologic form 60 and differed from any other races known at the time. Johnston (34) has also described an aberrant form of *P. triticina*.

The aecial host of rusts has been regarded by many students as a possible meeting-ground for various specialized races and thus

might serve as a bridge for the races to extend their host range. Arthur (3) came to the conclusion that the "barberry acts as a bridging host between each and every other gramineous host." Recent investigations support the view of special importance of the aecial host in physiologic specialization. If physiologic forms are heterozygous in the uredial stage, they may appear uniform and constant as long as cultivation by urediospores is continued. If, however, they pass over on to the aecial host, new combinations, with segregation, resulting in new capacities for infection of uredial hosts may occur. Further, if two forms differing in capacity for infecting uredial hosts hybridize on the aecial plant, new combinations may arise which may later be separated out through the aeciospores and perpetuated by the urediospores.

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REMARKS ON THE LIFE-HISTORY OF THE RHODOPHYCEAE

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In the Rhodophyceae the fertilized egg never separates from the motherplant but remains in intimate connection with it and by continued growth develops into a so-called gonimoblast. The gonimoblast generates a great many spores (carpospores) which disseminate in the water and give rise to new individuals. The gonimoblast receives practically all its nourishment from the motherplant and a great variety of organs are developed among the Florideae in order to facilitate supply of food to the gonimoblast. For classification of red algae those organs are very important and in a study of the lines of phylogenetical development in the Florideae it is essential to determine carefully the origin and structure of food-supplying organs.

Schmitz (22) early pointed out that sporogenous filaments of the Rhodophyceae connect themselves with nutritive cells in the motherplant and he calls these auxiliary cells. Later on Kylin (13) called attention to the fact that there are different kinds of auxiliary cells: those which are only nutritive cells and those which serve both as food-suppliers and as starting-points of the gonimoblasts. Kylin (14) calls the latter typical auxiliary cells. Typical auxiliary cells are found in the orders Cryptonemiales, Gigartinales, Rhodymeniales and Ceramiales, while in the orders Nemalionales and Gelidiales typical auxiliary cells do not occur but only various nutritive ones are found.

As a characteristic feature of the Nemalionales it can be pointed out that all food which the motherplant gives to the growing gonimoblast goes through the carpogonial branch. In the Nemalionales the gonimoblast is connected with the motherplant only by the carpogonial branch (concerning one exception see further on). The gonimoblast develops directly from the fertilized cargogonium (concerning one exception see further on).

As to development of the gonimoblast in the Nemalionales the following examples will be presented. In *Batrachospermum* the carpogonium, when fertilized, produces a number of filaments

which together form a gonimoblast. All food from the motherplant to the gonimoblast passes through the carpogonial branch whereby cells of the carpogonial branch become rather full of nutriment but do not fuse with each other. In *Nemalion* the carpogonium, after being fertilized, divides by a cross wall into two cells. The upper one gives rise to the gonimoblast, the lower one fuses gradually with the hypogynous cell which in turn fuses with the other cells of the carpogonial branch, and in this way there is formed a fusion cell full of food. Through this fusion cell food is transported from the motherplant to the gonimoblast. It is evident that this cell is of importance in the physiology of nutrition. The cell may be called an auxiliary one but it is not a typical auxiliary cell according to the terminology of Kylin. Wilke and Ziegenspeck (27) call it a carpogonium-auxiliary.

In *Scinaia* there are developed from the hypogynous cell four cells before fertilization which are rich in nutritive material. After fertilization the carpogonial nucleus enters into one of these nutritive cells and there reduction division takes place and four nuclei are formed. One of these nuclei proceeds to the carpogonium from which a gonimoblast develops. The food to the gonimoblast is supplied by the motherplant and passes through the carpogonial branch. There is no other connection between the gonimoblast and its motherplant. Svedelius (24) calls the four nutritive cells auxiliary cells. In my opinion they are, however, not typical auxiliary cells but carpogonium-auxiliaries in the sense of Wilke and Ziegenspeck.

In *Bonnemaisonia* there develops, before fertilization, from the hypogynous cell a bunch of filaments consisting of many nutritive cells. After fertilization there grows out from the carpogonium a gonimoblast which, in the early stage of its development, takes food from the nutritive cells. Thereby the carpogonium fuses with the hypogynous cell and this one in turn fuses with the nutritive cells. Only a small quantity of food is, however, transferred from the motherplant to the gonimoblast through the carpogonial branch and the gonimoblast, therefore, also connects itself with other nutritive cells in the motherplant; the gonimoblast, moreover, will not be fully developed until the food supply through the new connection is sufficiently rich. Thus, in *Bonnemaisonia* there are two different kinds of nutritive cells but there are no typical auxiliary

ones. The hypogynous cell as well as the nutritive cells that are developed from the former are carpogonium-auxiliaries. They serve during the early stage of the development of the gonimoblast. Those nutritive cells which serve in the mature stage of the development cannot be called typical auxiliary cells because the gonimoblast does not begin its development from them but from the carpogonium itself. It is, however, very interesting to note that the gonimoblast is connected with the motherplant in quite a different way than by the carpogonial branch.

Asparagopsis has recently been investigated thoroughly by Svedelius (26) who found that it conforms with *Bonnemaisonia* in many respects but also differs in several ways. In *Asparagopsis,* as in *Bonnemaisonia,* there is developed, before fertilization, a group of nutritive cells from the hypogynous cell. After fertilization the carpogonial nucleus proceeds into the hypogynous cell where reduction division occurs. After reduction division the gonimoblast grows out from the hypogynous cell which for food supply connects itself with the above-mentioned group of nutritive cells. Svedelius classifies the hypogynous cell as a typical auxiliary cell but according to my opinion this cell ought not to be called a typical auxiliary cell. I prefer to consider the hypogynous cell and the nutritive cells growing out from it as carpogonium-auxiliaries. During further development of the gonimoblast the cells in the carpogonial branch fuse with one another and with large nutritive cells belonging to the motherplant, forming a large fusion cell from which the gonimoblast then develops. There are similar nutritive cells in *Bonnemaisonia* but here food for the growing gonimoblast passes through a connection which has nothing to do with the carpogonial branch, while in *Asparagopsis* all food to the gonimoblast goes through the carpogonial branch.

In *Atractophora,* just as in *Asparagopsis* and *Bonnemaisonia,* we find a group of nutritive cells coming from the hypogynous cell. Together they form carpogonium-auxiliaries. In *Atractophora* these are, however, scarcely of any importance because the carpogonium, when developing, connects itself with the supporting cell of the carpogonial branch and thus, for its food-supply, enters into direct connection with the motherplant in another way than through the carpogonial branch. The supporting cell is of great physiological importance from an alimentary point of view but it

cannot be designated a typical auxiliary cell because the gonimoblast does not develop from it but from the carpogonium.

In the order Gelidiales there are developed, before fertilization, many food-containing filaments which closely wind round the central cells of the procarps. The gonimoblast grows out directly from the fertilized carpogonium and the growing filaments of the gonimoblast obtain their nutritive material from the food-containing filaments mentioned above. No typical auxiliary cells are to be found in this order. The Gelidiales belong to the diplobiontic Florideae. Reduction division occurs at development of tetraspores which are found on special plants. In Nemalionales reduction division occurs immediately after fertilization, perhaps with the exception of *Liagora tetrasporifera* (see further on). The Nemalionales belong to the haplobiontic Florideae.

In the order Cryptonemiales, Gigartinales, Rhodymeniales and Ceramiales the gonimoblast never develops from the fertilized carpogonium but the latter connects itself in some way or other with a cell in the motherplant and the gonimoblast develops from this, after having received a diploid nucleus. The cell from which development of the gonimoblast occurs is called a typical auxiliary cell by Kylin (14). In all Florideae with typical auxiliary cells direct connection is formed between the gonimoblast and the motherplant, and the carpogonial branch plays no part in transportation of nutritive material. Thus, the food-supply becomes more direct. A typical auxiliary cell never occurs in the carpogonial branch. Before fertilization the auxiliary cell may be rich in nutritive content but it is as frequently devoid of such material and is then not to be distinguished from surrounding vegetative ones.

Kylin (15) points out that there are several kinds of typical auxiliary cells. Formerly three types were distinguished but to these may now be added one more (the Rhodymenia type). Thus, there are the following four kinds of typical auxiliary cells:

(1) The Dumontia type: the auxiliary cells appear in special accessory branches which are developed before fertilization.

(2) The Platoma type: a normal intercalary cell of the motherplant serves as an auxiliary cell.

(3) The Rhodymenia type: the auxiliary cell is already cut off from a daughter cell of the supporting cell before fertilization.

(4) The Ceramium type: the auxiliary cell is cut off from the supporting cell of the carpogonial branch after fertilization.

The four kinds of typical auxiliary cells mentioned above are characteristic of the orders Cryptonemiales (the Dumontia type), Gigartinales (the Platoma type), Rhodymeniales (the Rhodymenia type) and Ceramiales (the Ceramium type), respectively.

The fertilized carpogonium may become connected with the auxiliary cell in various ways. In lower forms belonging to both the Cryptonemiales (*Dumontia, Dudresnaya, Grateloupia*) and the Gigartinales (*Platoma, Furcellaria, Agardhiella, Rhabdonia*) there are formed long and sometimes branched connecting filaments which transfer diploid nuclei from the carpogonium to many auxiliary cells lying rather remote from the carpogonium. In the higher forms of both the Cryptonemiales and Gigartinales no connecting filaments are formed but the fertilized carpogonium becomes connected directly with an adjacent, previously fixed, auxiliary cell (*Callymenia* and *Callophyllis* in the Cryptonemiales and *Cystoclonium, Calliblepharis, Hypnea, Phyllophora* and *Gigartina* in the Gigartinales). In this case the carpogonium and the auxiliary cell form a unit which is called a procarp. In the orders Rhodymeniales and Ceramiales procarps are always formed and as a rule there is a direct connection between the carpogonium and the auxiliary cell. Only in some of the more primitive species is a short one-celled (seldom two-celled) connecting filament formed (*Antithamnion, Callithamnion, Spermothamnion, Dasya*).

As stated above, typical auxiliary cells serve a double purpose of being both nutritive cells and starting points of gonimoblasts. Typical auxiliary cells never lose their function of being starting points of development of gonimoblasts, but they can lose their nutritive power. Sometimes they have a nutritive function only during the very first stages of the development of the gonimoblasts but are of no importance later on and seldom do not disappear totally. In such cases, there are other cells which succeed them in acting as a food-supplying medium. Some examples are cited below.

Cryptonemiales. In *Dumontia* and in *Dudresnaya* the gonimoblasts are comparatively small and food supplied through auxiliary cells is sufficient for their further development. The auxiliary cells do not fuse with the surrounding cells. In *Grateloupia* the

gonimoblast is somewhat larger than in the two above-mentioned species but even here all food is supplied through the auxiliary cell. This cell becomes large but it does not seem to fuse with surrounding vegetative cells. In *Callophyllis* the auxiliary cell is already large and rich in food before fertilization occurs. After fertilization the auxiliary cell develops a number of gonimoblast-filaments which, during the early stages of their development, obtain their food from the auxiliary cell. From the sterile tissue surrounding the procarp there develops, after fertilization, however, a large number of filaments which together form a kind of nutritive tissue into which the filaments of the gonimoblast grow. In its further development the gonimoblast is supplied with food from this nutritive tissue. In the full-grown gonimoblast the auxiliary cell has disappeared totally.

Gigartinales. In *Calosiphonia, Furcellaria* and *Halarachnion* all food to the gonimoblast passes through the auxiliary cell which becomes large and nutritive but does not fuse with the surrounding cells. In *Agardhiella, Solieria* and *Meristotheca* there is developed, after fertilization, a nutritive tissue of small cells around the auxiliary cell and the growing gonimoblast enters into direct connection with this tissue by special filaments. In *Cystoclonium* the auxiliary cell is of importance as a nutritive cell only during first stages of development of the gonimoblast. After fertilization fusion occurs between the auxiliary cell and surrounding vegetative cells. There is thus formed a large food-containing fusion cell through which food is conducted to the growing gonimoblast. In *Calliblepharis* as in *Hypnea* the auxiliary cell is of nutritive importance only during early stages of development of the gonimoblast. Later on the gonimoblast receives all food from special nutritive tissue which is developed after fertilization. In *Stenogramme, Phyllophora* and *Gigartina* the auxiliary cell is already large and nutritive before fertilization but its nutritive importance is limited, however, to the very first stages of development of the gonimoblast. In *Stenogramme* and *Phyllophora* the gonimoblast receives its food from nutritive tissue which is developed before fertilization occurs but in *Gigartina* a special tissue for the purpose of supplying the gonimoblast with food is developed after fertilization.

Rhodymeniales. In *Fauchea, Rhodymenia, Lomentaria* and *Chylocladia* the auxiliary cells, before fertilization, are small and similar to the surrounding vegetative cells and contain either just as much or only a little more food than the latter. But after fertilization they grow considerably and become filled with nutritive material. All food to the gonimoblast passes through the auxiliary cell. A fusion between the auxiliary cell and surrounding vegetative cells occurs sometimes.

Ceramiales. The auxiliary cell is here cut off after fertilization and is rich in food already from the beginning. The supporting cell, and often the central cell too, contains a large quantity of food. In addition there are present, as a rule, several very nutritious so-called sterile cells. A fusion occurs between the auxiliary cell, the supporting cell, and the first gonimoblast cell in an early stage of development of the gonimoblast. The fusion cell, thus formed, may later also fuse with other cells. All food to the gonimoblast is conducted through the fusion cell.

It has already been mentioned that a Floridean system which so far as possible has to show phylogenetical development has to be founded primarily on the auxiliary cells and the nutritive tissues. An outline of such a system is presented by Kylin (17). This system is based on statements of previous authors, on his own investigations and on papers by Sjöstedt and Bliding. After the above-mentioned outline of a Floridean system had been presented there appeared a paper by Rosenberg (19) in which he points out that the family Dasyaceae forms an independent group in the order Ceramiales. The Dasyaceae were formerly classified as belonging to the family Rhodomelaceae. In a paper which appeared in 1934, Kylin has shown that in the Rhodomelaceae the carpogonial branch is cut off later than the lateral group of the so-called sterile cells. Previously the carpogonial branch was always considered to be cut off before the sterile cells. The observations of Kylin show that, viewed from the history of development, the four families Ceramiaceae, Delesseriaceae, Dasyaceae and Rhodomelaceae are all closely related to each other.

Concerning alternation of generations in the Florideae two types are distinguished by Svedelius (24): the haplobiontic type and the diplobiontic type. In the latter type, there is in the life-history a regular alternation between individuals bearing gonimoblasts and

those bearing tetraspores. In the former (haplobiontic) type special individuals bearing tetraspores are lacking. In the haplobiontic Florideae reduction-division occurs at the first division of the fertilized nucleus (usually in the carpogonium), but in the diplobiontic forms it takes place, on the contrary, at formation of the tetraspores. Investigations of recent years have, however, revealed some exceptions of great interest to this general rule.

The haplobiontic Florideae belong to the order Nemalionales. To this order also belongs the genus *Liagora.* Börgesen (2) discovered, however, that in one species of this genus, *L. tetrasporifera,* the gonimoblast develops tetraspores instead of carpospores (monospores). Later Kylin (15) verified this statement. It is not known where reduction division takes place in *Liagora tetrasporifera* but it is not at all improbable that it is removed from the carpogonium to the tetrasporangia and in that case the gonimoblast would be diploid, not haploid as in the haplobiontic Florideae.

It has already been known for a long time that *Phyllophora Brodiaei* bears small globular bodies which produce tetraspores. These bodies have been supposed to belong to a parasitic Florideae, called *Actinococcus subcutaneus.* No generative organs were, however, ever observed in *Phyllophora* and some investigators thus declared *Actinococcus* to be nothing but the generative organs of *Phyllophora.* The problem was solved recently by Rosenvinge (20) since he was able to show that *Actinococcus* originates from the auxiliary cell of *Phyllophora.* In *Phyllophora* only sexual individuals are to be found. The auxiliary cells which ought to grow out to gonimoblasts with carpospores (monospores) give rise instead to small globules which produce tetraspores. It could be expressed as follows: formation of carpospores is replaced by formation of tetraspores. According to Claussen (7) reduction division occurs at formation of tetraspores. In *Phyllophora Brodiaei* there are no independent tetrasporic plants. From a systematic point of view *Phyllophora* belongs to the diplobiontic Florideae but in its life-history it is, however, a haplobiontic Florideae, very comparable to *Liagora tetrasporifera.* In another species, *Ph. membranifolia,* there are independent tetrasporic plants as well as plants with gonimoblasts. *Ph. membranifolia* is a typical diplobiontic Florideae. The statement of Rosenvinge concerning *Ph. Brodiaei* has been verified by Kylin (15).

With respect to alternation of generations, the conditions in *Phyllophora* have parallels in the genus *Gymnogongrus*. There are, for example, in *G. norvegicus* both individuals with tetraspores and individuals with gonimoblasts. *G. norvegicus* corresponds to *Phyllophora membranifolia*. In *Gymnogongrus Griffithsiae* only tetrasporic individuals occur. The tetraspores are here produced in small globular bodies which formerly were considered as an independent species, *Actinococcus aggregatus*. Quite recently, Chemin (6) and Gregory (9) stated that *G. Griffithsiae* is a sexual plant and that *Actinococcus aggregatus* is developed from auxiliary cells of *Gymnogongrus Griffithsiae* and that it represents the tetrasporic generation of this alga. *G. Griffithsiae* is a parallel to *Phyllophora Brodiaei*.

The small globular bodies on *Ahnfeltia plicata* were formerly regarded as being a parasitic red alga, *Sterrocolax decipiens*. The globular bodies produce monospores as reproductive organs. Formerly no reproductive organs were known to occur in *Ahnfeltia*. Now, however, Chemin (5), Rosenvinge (21) and Gregory (9) have all been able to show that *Sterrocolax decipiens* represents the reproductive organs of *Ahnfeltia plicata*. It seems, however, that sexual reproduction is lacking in *Ahnfeltia* and that *Sterrocolax* in an asexual manner grows out from *Ahnfeltia*. The fact that *Sterrocolax* gives rise only to monospores and not to tetraspores is obviously connected with the fact that there is no sexual reproduction in *Ahnfeltia*. Individuals of *Ahnfeltia* which bear the *Sterrocolax*-globules represent female individuals. Special male individuals with spermatangia are found also in *Ahnfeltia*.

In the diplobiontic red algae there is regular alternation between haploid sexual individuals and diploid asexual ones. Haploid individuals are bearers of gonimoblasts, diploid ones of tetraspores. Sometimes, however, gonimoblasts and tetraspores occur on the same individuals. The best known species in which this condition is found is *Spermothamnion Turneri* (Sp. *roseolum*). This alga has recently been studied by Kathleen Drew (8) with special reference to cytological facts. From results of her studies the following facts are to be noted. All individuals found growing in the sea were diploid with 60 as the number of chromosomes. Those individuals bore tetraspores as well as fully developed gonimoblasts. In formation of tetraspores reduction divisions took place. The

nuclei of the developing gonimoblast showed it to be tetraploid. Whether the tetraploid carpospores are capable of germination or not was not investigated. When cultivated, the haploid tetraspores germinated into haploid filaments which, however, died when they were three or four cells in length. The statement that the developing gonimoblast is tetraploid is of special interest. It is evident, however, that further investigations are necessary before the problem of the alternation of generations in *Spermothamnion* can be solved.

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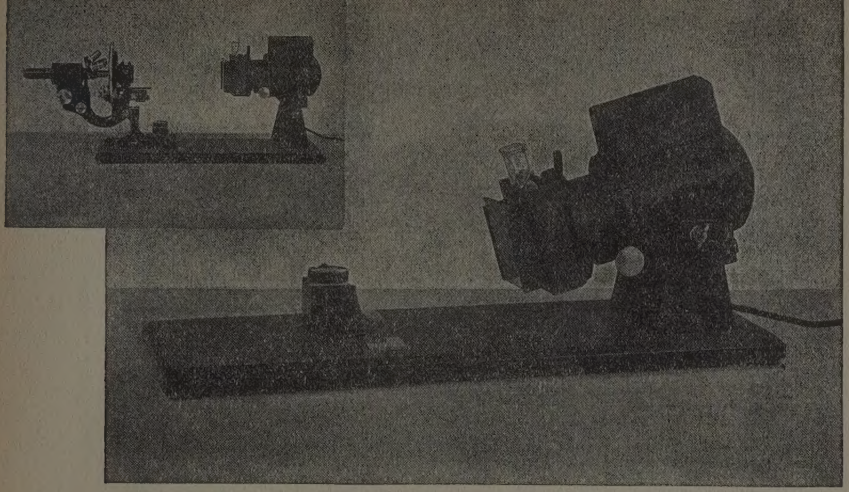
Glossary

The Rhodophyceae, or Red Algae, are known also as the Florideae; this name, as used by some authors, however, excludes one order, the Bangiales. The great majority of red algae are marine; only a few inhabit fresh waters. Their sexual reproduction is quite unlike that of any other algae and has necessitated special terminology, use of which varies somewhat among different writers. In general, however, the following brief discussion will serve as a basis for the accompanying article.

The male organs, *antheridia*, produce non-motile *spermatia*. The female organ, *carpogonium*, is borne on the *carpogonial branch* and has an elongated receptive *trichogyne*. The *egg* is at the base of the *carpogonium* and after fertilization does not develop into a new plant but produces *carpospores* in a variety of ways. These spores develop directly from the zygote, or from *sporogenous filaments* which arise from the zygote and constitute the *gonimoblast*. They may also develop from other cells of the thallus into which the zygote nucleus or one of its descendants has migrated. The entire spore-producing structure is known as a *cystocarp*. The *hypogynous cell* is the one immediately below the *carpogonium*.—Editors.



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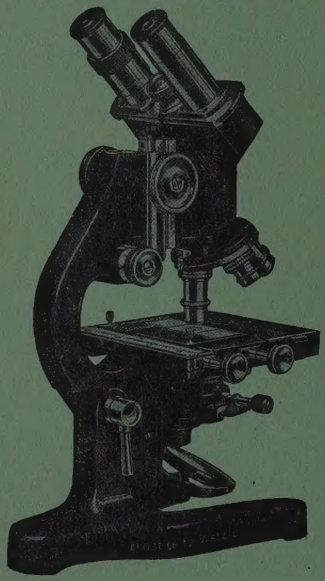

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